Neuroscience and Biobehavioral Reviews 36 (2012) 1273–1291

Contents lists available at SciVerse ScienceDirect

Neuroscience and Biobehavioral Reviews

journal homepage: www.elsevier.com/locate/neubiorev

Review

Left–right asymmetries of behaviour and nervous system in invertebrates

Elisa Frasnelli[a,*], Giorgio Vallortigara[b], Lesley J. Rogers[c]

[a] Konrad Lorenz Institute for Evolution and Cognition Research, Adolf Lorenz Gasse 2, A-3422 Altenberg, Austria
[b] CIMeC, Centre for Mind/Brain Sciences, University of Trento, Corso Bettini 31, 38068 Rovereto, Italy
[c] Centre for Neuroscience and Animal Behaviour, University of New England, Armidale, NSW 2351, Australia

ARTICLE INFO

Article history:
Received 26 September 2011
Received in revised form 25 January 2012
Accepted 6 February 2012

Keywords:
Brain asymmetry
Laterality
Invertebrates
Lateralization of behaviour
Brain lateralization
Evolution of lateralization

ABSTRACT

Evidence of left–right asymmetries in invertebrates has begun to emerge, suggesting that lateralization of the nervous system may be a feature of simpler brains as well as more complex ones. A variety of studies have revealed sensory and motor asymmetries in behaviour, as well as asymmetries in the nervous system, in invertebrates. Asymmetries in behaviour are apparent in olfaction (antennal asymmetries) and in vision (preferential use of the left or right visual hemifield during activities such as foraging or escape from predators) in animals as different as bees, fruitflies, cockroaches, octopuses, locusts, ants, spiders, crabs, snails, water bugs and cuttlefish. Asymmetries of the nervous system include lateralized position of specific brain structures (e.g., in fruitflies and snails) and of specific neurons (e.g., in nematodes). As in vertebrates, lateralization can occur both at the individual and at the population-level in invertebrates. Theoretical models have been developed supporting the hypothesis that the alignment of the direction of behavioural and brain asymmetries at the population-level could have arisen as a result of social selective pressures, when individually asymmetrical organisms had to coordinate with each other. The evidence reviewed suggests that lateralization at the population-level may be more likely to occur in social species among invertebrates, as well as vertebrates.

Contents

* Corresponding author.
E-mail address: elisa.frasnelli@kli.ac.at (E. Frasnelli).

0149-7634/$ – see front matter © 2012 Elsevier Ltd. All rights reserved.
doi:10.1016/j.neubiorev.2012.02.006

1. Introduction

Brain lateralization (i.e. different functional and/or structural specializations of the left and right sides of the brain), once considered to be unique to humans (Corballis, 1989), is now well known to be present in all vertebrate classes (reviewed by Rogers and Andrew, 2002; Vallortigara and Rogers, 2005; MacNeilage et al., 2009; Vallortigara et al., 2011). Recently, evidence of lateralization in invertebrates has begun to emerge, suggesting that lateralization of the nervous system may be a feature of simpler brains as well as more complex ones.

A variety of left–right asymmetries in general morphology has been observed among invertebrates (reviewed by Palmer, 2009) but here we focus on asymmetries in the nervous system and behaviour. Knowledge of invertebrate asymmetries may be crucial to understanding the evolution of brain asymmetry and, given the relative simplicity of some of their brains, invertebrates could provide excellent model systems to investigate molecular, genetic and developmental aspects of lateralization. We address all of these aspects in our review.

The fossil record of animals contains numerous examples of handedness. Babcock (1993) reported examples of morphological or behavioural asymmetry from representatives of the Arthropoda, Annelida, Bryozoa, Echinodermata, Cnidaria, Mollusca, Chordata, and Conodonta. Behavioural asymmetry is seen in predation scars on fossils of trilobites: these scars are more commonly located on the right side than on the left (Babcock, 1993). Sixty specimens (70%) showed injuries only on the right pleural lobe, compared to 23 specimens that had injuries only on the left. Three specimens (3%) had injuries on both sides. This suggests that some predators of trilobites may have attacked the right sides of trilobites, or that the trilobites themselves exhibited an asymmetry in stereotyped escape behaviour. That some of the earliest trilobites or their predators exhibited right–left differences in behaviour suggests that lateralized nervous systems were in existence by the Early Cambrian, i.e. for more than 500 million years.

In this paper we review evidence of asymmetries in extant invertebrates species: Arthropoda (Insecta, Arachnida, Malacostraca), Mollusca (Gastropoda, Cephalopoda) and Nematoda (*Caenorhabditis elegans*).

2. Arthropoda: Insecta, Arachnida, Malacostraca

2.1. Hymenoptera: Apidae

2.1.1. Honeybees

Honeybees (Insecta, Hymenoptera, Apidae, Apinae, Apini) have provided evidence of lateralization in sensory systems, particularly of olfaction. Letzkus et al. (2006) first showed that honeybees (*Apis mellifera*) display laterality in learning to associate an odour with a sugar reward. The researchers used the proboscis extension reflex (PER) paradigm (Bitterman et al., 1983), in which bees are conditioned to extend their proboscis when they perceive a particular odour that has been associated with a food reward. They tested bees in two versions of the PER paradigm: (1) honeybees were conditioned to extend their proboscis to a scented drop of sugar water but not to an unscented drop of salt water, (2) honeybees were conditioned to extend their proboscis to one odour (dissolved in a sugar solution – reward) but not to another odour (dissolved in a salt solution – punishment). Each version of the learning task was carried out on three groups of bees comprised at least 70 2-week-old bees. The bees in one group had their left antenna covered with a silicone compound, which prevents detection of odour, those in the second group had their right antenna covered, and those in the third group constituted a control in which both antennae were uncovered. Tests were carried out on the morning after the training had been performed. Results revealed that the bees with the right antenna covered learnt less well than the bees with their left antenna covered and bees with both antenna uncovered. In fact, the bees trained with only their right antenna in use performed just as well as the untreated controls.

It is difficult to understand whether this particular lateralization is due to a sensory asymmetry in the antennae or to a difference in learning or memory recall between the right and the left olfactory pathways. Letzkus et al. (2006) compared the number of the olfactory receptor sensory organs, *sensilla placodea*, in the two antennae. Images of 10 right antennae and 10 left antennae (seven of these left–right pairs originated from the same individuals) were obtained using scanning electron microscopy (SEM) and the mean numbers of *sensilla placodea* per flagellum on the two antennae were compared. The number was significantly higher on the right than on the left antenna (mean difference of 10%). This finding should be interpreted with caution, however, since only one type of sensilla was considered, and there are other sensilla, such as *sensilla trichodea* (Dietz and Humphreys, 1971), which play an olfactory role in honeybees. Moreover, in the paper of Letzkus et al. (2006), SEM images did not cover the whole antennal segment surface leaving a hidden, non-characterized area. Finally, only 7 out of 10 left–right pairs of antenna were from the same individuals.

In a recent study, however, Frasnelli et al. (2010b) duplicated the behavioural results of Letzkus et al. (2006) using forager Italian honeybees (*Apis mellifera ligustica* Spin.) and checked for morphological differences in the number of sensilla between the right and the left antenna of 14 honeybees. Both antennae of each bee were imaged from four different perspectives and all of the different types of sensilla were considered. Results showed that putative olfactory sensilla (*placodea*, *trichodea*, *basiconica*) were significantly more abundant on the right antenna surface than on the left antenna surface (mean difference of 3%), whereas sensilla not involved in olfaction (*campaniformia*, *coeloconica*, *chaetica*) were more abundant on the left than on the right antenna surface (mean difference of 7%), apart from on the tenth segment where no difference was observed. In another study, Anfora et al. (2010) recorded the electroantennographic (EAG) responses (that is a measure of the electrical signal over a section of the antenna) of honeybees' antennae stimulated with two different scents. The EAG responses to both a floral volatile compound and to an alarm pheromone were higher in the right than in the left antenna (mean difference of 18% for the floral volatile compound and 20% for the alarm pheromone). Thus, in honeybees, the higher electrophysiological response of the olfactory receptor neurons in the right antenna (Anfora et al., 2010) seems to correspond to a greater number of the olfactory sensilla on the right antenna compared to the left antenna (Letzkus et al., 2006; Frasnelli et al., 2010b).